

Functional Dental Correlates of Food Properties in Five Malagasy Lemur Species

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ABSTRACT Biomechanical explanations are fundamental to studies of functional dental morphology. Until recently foods were not classified in mechanical categories amenable to a rigorous examination of the fundamental physical relationship between teeth and foods. Fruit, insect and leaf categories, although descriptive, are mechanically heterogeneous. The diets of five Malagasy lemur taxa were described in terms of two mechanical properties, hardness and shear strength, in an earlier study (Yamashita, 1996b). In the present study, correlations between these two physical food properties and second molar tooth features of two lemur families are examined. Several relationships are hypothesized: 1) crest length is expected to be positively correlated with food shear strength; 2) the radius of curvature (r) of cusps is expected to be positively correlated with food hardness; and 3) basin area should increase relative to cusp radius as food hardness increases, and cusp-to-basin ratios should decrease with increasing food hardness. Two additional hypotheses address the debate concerning the relative influences of the most frequently eaten foods versus the most stressful foods in determining tooth form. The results of the predicted relationships are equivocal. 1) Crest length is negatively instead of positively correlated with strong foods. Crest lengths are correlated with quantities of leaf consumption, which are related to leaf shape more than to material composition. 2) As expected, r is positively correlated with food hardness and negatively with shear strength, but this applies to upper molar cusps only. Lower molar cusps complicate simple generalizations of relationships. 3) Hard foods are correlated with a tight fit of occluding cusps and basins instead of the expected loose fit. The most stressful foods eaten (hardest and strongest) have higher correlations with tooth features than the most frequently eaten foods. Several functional complexes can be identified. Hard food items are correlated with short cusps in lemurids, tight occlusal fit, small trigon and large talonid areas, and deep, acute basins. Large, shallow trigons, shallow, unrestricted talonids, and large upper molar basins are indicative of a diet of strong foods. These results demonstrate that some variation in tooth features is explicable with reference to mechanical properties of diet, although the relationships are complex. *Am J Phys Anthropol* 106:169–188, 1998. © 1998 Wiley-Liss, Inc.

Comparative studies of tooth form in primates have identified specific features that vary consistently with respect to the basic dietary categories of insects, fruits, and leaves (Seligsohn and Szalay, 1974, 1978; Hylander, 1975; Kay, 1975, 1977, 1978, 1984; Rosenberger and Kinzey, 1976; Seligsohn,

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1977; Kay and Hylander, 1978; Kay et al., 1978; Kinzey, 1978; Maier, 1984; Happel, 1988; Strait, 1993a). The physical properties of these foods are hypothesized to be important selective factors operating on tooth features. In this manner, long molar crests have been related to food toughness associated with folivorous or insectivorous diets (Kay, 1975; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Kay et al., 1978; Kinzey, 1978; Seligsohn and Szalay, 1978; Strait, 1993b), and food hardness has been linked to both thick enamel and low, rounded cusps in *Cebus* (Rosenberger and Kinzey, 1976; Kay, 1981). In addition, Seligsohn and Szalay (1978) related the acute cusps, short crests, and deep, confined basins of *Hapalemur griseus* to its diet of bamboo stems, and, in a study conducted by Seligsohn (1977), frugivorous and gummivorous strepsirhines possessed low, blunt cusps, short crests, and shallow basins.

These studies demonstrated that tooth form has some relationship to the physical or mechanical properties of the foods triturated. In other words, the primary relationship between teeth and foods is a physical one. In order to break down foods, teeth must stress the food to the point of fracture such that new surfaces are created for further digestion in the gut. The mode of failure will depend on the material properties and shape of the food, as well as the way in which stresses (loads) are applied.

Lucas et al. (1986) subdivided physical properties of foods into internal and external properties. Internal properties describe aspects of material composition that resist breakdown, such as strength, fracture toughness, and deformability. External properties include size, volume, shape, roughness, stickiness, and abrasiveness.

The majority of functional dental studies have not tested physical properties of foods directly (but see Happel, 1988; Strait, 1993b), relying instead on literature reports of diets placed in the three major food categories. The constituent foods in these categories are not homogeneous in material composition, however, and for this reason their use in studies of functional dental morphology has been questioned (Kay, 1975; Rosenberger and Kinzey, 1976; Lucas, 1979; Lucas and

Luke, 1984; van Roosmalen, 1984; Lucas et al., 1985; Rosenberger, 1992). Only recently have field studies been conducted on primate diets in which the physical properties of the foods have been the primary focus of interest (Happel, 1988; Kinzey and Norconk, 1990, 1993; Lucas and Teaford, 1994; Hill and Lucas, 1996; Strait and Overdorff, 1996; Yamashita, 1996a,b).

In a previous study, I tested hardness and shear strength of the diets of five lemur taxa in two families following observations of their diets in the field (Yamashita, 1996b). Hardness is defined as resistance to indentation, and the contrasts are between hard foods and soft foods. Shear strength is a measure of the breaking stress of a material placed under a shearing load. The contrasts for foods tested for shear strength are strong versus weak. Though lemur teeth have been well described (Seligsohn and Szalay, 1974, 1978; Seligsohn, 1977; Tattersall, 1982; Schwartz and Tattersall, 1985), quantification of tooth features has been limited (but see Covert [1986] for measurements of prosimian shearing quotients). In this study, I examine correlations between two components of the functional equation: measurements of tooth features and food properties.

HYPOTHESES

Using the dietary classifications in Yamashita (1996b), several predictions can be made concerning molar morphologies. The null hypothesis is that, given the variety of food types in lemur diets and variations in tooth morphology, lemurids and indriids demonstrate no biomechanically predictable pattern of relationships between the physical properties of their foods and tooth morphology.

Alternatively, 1) crest length is positively correlated with food shear strength. *Elasticophagus* taxa, which consume tough and/or soft foods, should have long crests or blades that encourage continued crack propagation (Kay et al., 1978; Lucas, 1979; Lucas and Luke, 1984).

2) The radius of curvature (r) of cusps is positively correlated with the hardness of foods. The molars of *durophagus* taxa (which eat hard, brittle foods) are predicted to have short, blunt cusps and basins that are large

enough to allow for lateral excursions of the cusp tips that occlude into them (Rosenberger and Kinzey, 1976; Seligsohn, 1977; Lucas, 1979). Blunt cusps have a large surface area which enable them to induce run-away crack propagation on the food surfaces to which they are applied (Lucas, 1979). Moreover, if cusps are free to move in basins, hard, brittle foods can be moved until their weakest points are located and exploited (Lucas and Luke, 1984). Basin area should be large relative to the acuity of the occluding cusp tip, but the cusp cannot be so acute as to be unable to handle the stresses of triturating hard food particles.

3) Following from (2), basin area increases relative to cusp radius as food hardness increases. Cusp-to-basin ratios decrease with increasing food hardness.

Other key points involve the relative influences of the most frequently eaten foods versus the most stressful foods in determining tooth form. Primate species have been assigned to major dietary categories based on overall percentage intake of particular foods. Kay (1975) stated that an animal must ingest 45% or more of a food before its mechanical properties would have an impact on its tooth morphology. Although acknowledging the importance of the primary diet to tooth form, Kinzey (1978) and Rosenberger and Kinzey (1976) argued for the importance of secondary dietary items to tooth form. Foods that do not form the bulk of the diet may be critical at certain times of the year when resources are scarce. In this scenario, teeth perform a "critical function," enabling animals that can process certain foods to survive a marginal dietary period. This issue is framed in the current study as:

4) The radius of curvature of cusp tips is more highly correlated with the hardest food eaten than with the hardness value of the most frequently eaten food.

5) Crest length is more highly correlated with the shear strength of the strongest food eaten than with the most frequently eaten food.

MATERIALS AND METHODS

Diets of *Lemur catta* (Lc), *Lemur fulvus rufus* (Lfr), *Lemur rubriventer* (Lr), *Propithecus diadema edwardsi* (Pde), and *Propithecus v. verreauxi* (Pvv) were observed and

TABLE 1. Sample sizes of lemur taxa measured

	Sample size ¹ : museum (field specimen)
Superfamily Lemuroidea	
Family Lemuridae	
<i>Lemur catta</i>	24
<i>Lemur coronatus</i>	10
<i>Lemur fulvus albifrons</i>	10
<i>albocollaris</i>	3
<i>collaris</i>	8
<i>fulvus</i>	10
<i>mayottensis</i>	10
<i>rufus</i>	15 (2)
<i>sanfordi</i>	5
<i>Lemur macaco</i>	10
<i>Lemur mongoz</i>	10
<i>Lemur rubriventer</i>	24 (4)
<i>Lemur variegatus rubra</i>	4
<i>variegatus</i>	6
Family Indriidae	
<i>Avahi l. laniger</i>	10
<i>Indri indri</i>	10
<i>Propithecus diadema candidus</i>	7
<i>diadema</i>	8 (2)
<i>edwardsi</i>	10 (9)
<i>holomelas</i>	3
<i>Propithecus verreauxi coquereli</i>	10
<i>coronatus</i>	8
<i>deckeni</i>	10
<i>verreauxi</i>	25 (1)

¹ Species studied in the field are in bold.

tested for two food properties in two seasons of field work in Ranomafana National Park and Beza Mahafaly special reserve, Madagascar. Hardness and shear strength were the two food properties tested with portable apparatuses. Hardness was measured as puncture resistance for fruits, seeds, and succulents. Force readings from an A-type durometer were converted to pressure readings in kg/mm². Shear strength is stress at failure and is measured as punch shear with a punch tester in units of kg/mm² for leaf material, fruit skins, and flower parts. Measurements and protocols for testing food properties in the field are further detailed in Yamashita (1996b).

In addition to the five taxa studied in the field, upper and lower second molars of all taxa in the Lemuridae and Indriidae were measured to the subspecific level (Table 1) following the classification in Tattersall (1993). Several taxa are not represented because of lack of available, unworn samples; e.g., *Avahi laniger occidentalis* [elevated to *Avahi occidentalis* in Mittermeier et al. (1994)], *Propithecus diadema perrieri*, and

Propithecus tattersalli. The additional members of both families were measured to provide a context for tooth measurements of the field taxa and to determine variation within and between families that could potentially complicate a strictly functional interpretation of variance.

T-tests were conducted between field and museum specimens to determine if specimens measured in the field differed from populations of the same taxon from museum collections and if measuring techniques produced consistent values between the two populations. Most features were found to be similar between the two populations which were then pooled in subsequent analyses. Cusp heights in the indriid taxa, however, were underestimated in the field taxa owing to interference from the gum line and were removed from further analyses.

The sample was limited to adult specimens determined by complete eruption of the third molar. Although the morphology and tooth use of anterior teeth have been demonstrated to vary with diet (Hylander, 1975; Kinzey, 1992; Ungar, 1994), the postcanines are responsible for triturating food. Among the molars, the third molar varies in size by taxa (Schwartz and Tattersall, 1985). Second molars were chosen for study because of their intermediate position in the molar row.

Casting procedures

Tooth features were measured from epoxy tooth casts made from museum dental collections. Impressions of upper and lower occluding postcanine tooththrows were made with "President Jet regular body," a silicone-based dental impression material (Coltene-Whaledent). Impressions were made of the right side of the jaw unless teeth were missing in which case the opposite side was used. Casts were made of the upper and lower postcanine tooththrows of the same side (occlusal postcanine pairs) from Epo-Kwik, a fast-cure epoxy resin. In the field, the teeth of captured animals were cleaned, then air-dried prior to making the impression (as per Teaford and Glander, 1991). Impressions of only the lower tooth row were made of field specimens.

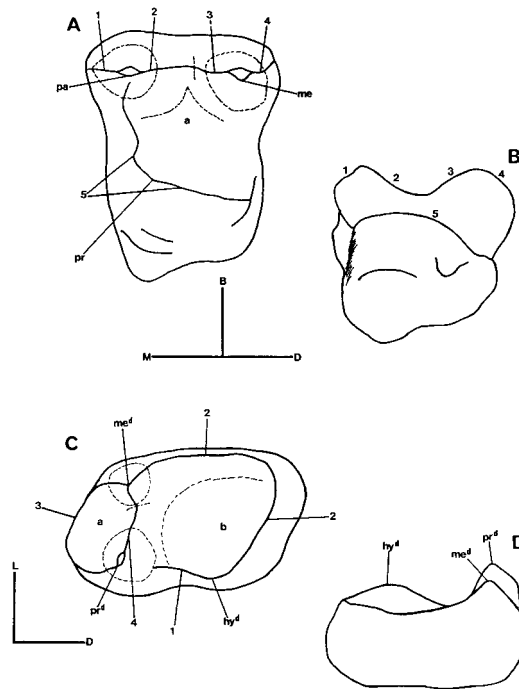


Fig. 1. Tooth features of left second molars measured for *Lemur rubriventer*. A: Occlusal surface of M². B: Three-quarter lingual view of M² demonstrating relief of cusps and crests. C: Occlusal view of M₂. D: Lingual view of M₂. Upper molar: 1, preparacrista; 2, postparacrista; 3, premetacrista; 4, postmetacrista; 5, protocristae; a, trigon; pa, paracone; me, metacone; pr, protocone. Lower molar: 1, cristid obliqua; 2, postcristid + preentocristid + postmetacristid; 3, paracristid; 4, protocristid; a, trigonid; b, talonid; pr^d, protoconid; hy^d, hypoconid; me^d, metaconid. M, mesial; D, distal; L, lingual; B, buccal.

Measuring protocols

Tooth areas, basin areas, crest lengths, radii of curvature of cusps, cusp heights, and ratios of occluding cusps and basins were measured from second upper and lower molars (Figs. 1, 2). Skull length was measured from prosthion to opisthocranium in mm for use as a potential size surrogate. Measuring protocols for the dentition are detailed below. Lists of field and museum specimens are in Table 1.

Tooth features were measured with JAVA (Jandel Video Analysis software) and a Reflex microscope. Procedures and protocols are reported in Yamashita (1996a). JAVA measures video images in two dimensions either via edge-tracking software that follows contours based on the contrast of the

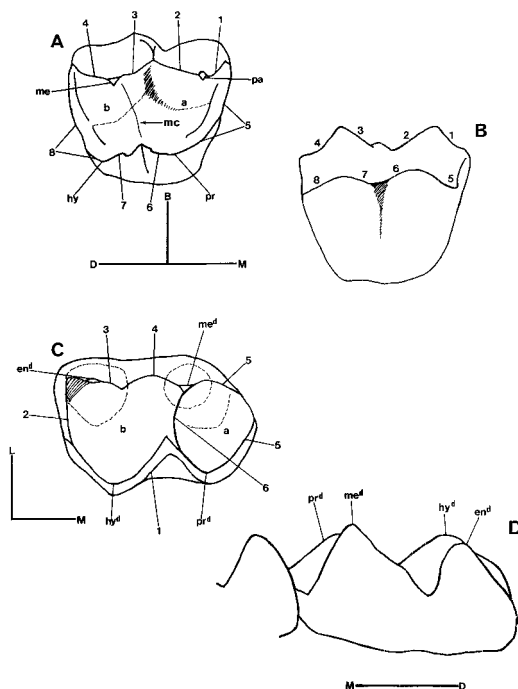


Fig. 2. Tooth features of right second molars measured for *Propithecus diadema edwardsi*. **A:** Occlusal surface of M_2 . **B:** Three-quarter lingual view of M_2 demonstrating relief of cusps and crests. **C:** occlusal view of M_2 . **D:** Lingual view of M_2 . Upper molar: 1, preparacrista; 2, postparacrista; 3, premetacrista; 4, postmetacrista; 5, preprotocrista; 6, postprotocrista; 7, prehypocrista; 8, postcingulum; a, trigon; b, talon; pa, paracone; me, metacone; pr, protocone; hy, hypocone; mc, middle crest. Lower molar: 1, cristid obliqua; 2, postcristid; 3, pre-entocristid; 4, postmetacristid; 5, paracristid; 6, protocristid; a, trigonid; b, talonid; pr^d , protoconid; hy^d , hypoconid; me^d , metaconid; en^d , entocoid. M, mesial; D, distal; L, lingual; B, buccal.

image or by tracing them manually from the keyboard. Teeth were oriented so that the plane of the occlusal surface of the second molar was parallel with the videocamera lens. Replicability tests of area measurements were conducted on *L. catta* trigon area ($n = 10$ trials). The percent error was 8%.

Measurements in three dimensions were obtained with a Reflex microscope. A high-intensity LED point acts as the measuring mark at the center of the microscope view. The microscope digitizes X, Y, and Z coordinates of individual points in conjunction with a measuring program, COMP 3D, that contains workfiles with instructions for desired measurements. Crest lengths, cusp heights, and cusp radii were measured with

the Reflex scope. Replicability tests for the microscope were performed by repeated measurement ($n = 10$) of the cristid obliqua in *P.v. verreauxi* and *L. rubriventer*. Errors were 7% and 5%, respectively.

Specific measurements

Crest lengths. Crest lengths were measured in mm with a Reflex microscope. Multiple points along a crest were digitized in order to incorporate changes in direction and slope of the crest that would be missed by measuring only two endpoints. The shorter linear distances were then summed to obtain the length of the crest. Cusp tips were considered the endpoints of the crests. The crests detailed below were measured for each individual.

Lemurid M_2 crests: Preparacrista, postparacrista, premetacrista, postmetacrista, protocristae (continuous pre- and postprotocristae) (Fig. 1A,B).

M_2 crests: Cristid obliqua; continuous crest including postcristid, pre-entocristid, postmetacristid; paracristid; protocristid (Fig. 1C). In addition, *L. variegatus* subspecies have a postprotocristid that extends from the protoconid buccally to meet the cristid obliqua at the hypoflexid notch; this crest was incorporated into the measurement of total crest length. *L. catta* has a lingual notch and a distinct entoconid lacking in the other lemurs that interrupts the continuous crest. M_2 crests measured for *L. catta* were cristid obliqua, postcristid, pre-entocristid, postmetacristid, paracristid, and protocristid.

Indriid M_2 crests: Preparacrista, postparacrista, premetacrista, postmetacrista, preprotocrista, postprotocrista, prehypocrista, postcingulum (Fig. 2A,B).

M_2 crests: Cristid obliqua, postcristid, pre-entocristid, postmetacristid, paracristid, protocristid (Fig. 2C). *Indri indri* has bilophodont crests that join the metaconid and protoconid mesially and entoconid and hypoconid distally. In addition, *Avahi* has a distinct crest joining the cristid obliqua and the protoconid that is not present in the other indriids and which resembles a postprotocristid. This crest was incorporated into measurements of lower molar crest length.

Basin areas. Areas of two-dimensional contours were calculated with JAVA in mm². The perimeters of the basins were demarcated by the crests noted below. Because crests are not straight lines (see above), their nonlinear distances were digitized. Indriids and lemurids differed in the presence or absence of some tooth features.

Trigon (both families). In lemurids, the basin is bounded mesially and lingually by the protocristae, which is a continuous ridge containing the protocone and pre- and postprotocristae; distally by the postprotocrista when present (postprotocrista is not well developed or is absent in all but *L. catta*); buccally by the centrocrista (postparacrista + premetacrista). In the lemurids except *L. catta*, the trigon is open distally (Fig. 1A). In these cases, the trigon was closed by the straight line distance between the end of the protocristae and the most distal point of the postmetacrista.

In indriids, the basin is bounded mesially by the preprotocrista, disto-lingually by the postprotocrista + a consistent middle fold (mc), buccally by the preparacrista + postparacrista (Fig. 2A).

Talon. This basin is only present in indriids. It is bounded mesially by the middle crest, distally by the postcingulum, buccally by the pre- and postmetacristae (Fig. 2A). The consistent middle crest may be what Tattersall (1982:152) describes as a "small transverse crease representing the anterior fovea."

Trigonid. In indriids the basin is bounded mesially by the paracristid, distally by the protocristid (Fig. 2C). Although lemurids also have this basin, it was not measured because the basin is not oriented on the same occlusal plane as the talonid.

Talonid (both families). In lemurids, the talonid is bounded mesially by the protocristid, buccally by the cristid obliqua; lingual and distal borders are one continuous crest (postcristid + preentocristid + postmetacristid) in all but *L. catta*, which has three crests (Fig. 1C).

In indriids, the basin is bounded mesially by the cristid obliqua and the protocristid starting at its intersection with the cristid

obliqua, distally by the postcristid, lingually by the postmetacristid + (pre) entocristid (Fig. 2C).

Because of the presence of the transverse crests, *Indri indri* has three fovea on the M₂. The mesial basin forms a single basin with the distal portion of the M₁ basin in which the M¹ hypocone occludes. The middle basin occludes with the M² protocone, and the distal M₂ basin forms a continuous basin with the mesial portion of the M₃ basin in which the M² hypocone occludes. Because of the occlusal relationships, the middle basin was measured as the talonid, and the other mesial and distal basins were measured separately and added together as the trigonid.

Tooth areas. Upper and lower second molar areas were measured as the entire outline of the tooth as depicted in (Figs. 1A,C, 2A,C). Tooth areas were measured with JAVA in mm² in the same orientation as the basin.

Cusp heights. Heights of cusps were measured as the linear distance in mm from the cusp tip to the cervix by the Reflex microscope. The cusps were measured either buccally or lingually depending on the position of the cusp.

M² cusps: Paracone, metacone, protocone, (hypocone in indriids only) (Figs. 1B,2B).

M₂ cusps: Protoconid, hypoconid, metacoenid, (entoconid in indriids and *L. catta* only) (Figs. 1, 2D)

Radius of curvature. The radius of curvature (*r*) is a measure of the radius of the circle of best fit into a cusp tip. Deriving *r* is predicated on the fact that any three nonlinear points describe a circle. Three points were measured on cusps by the Reflex microscope (Fig. 3). The first point (A) was at the apex of the cusp; the other two points (B, C) were taken lateral to the apex. Linear distances in mm between all points and angles of the triangle ABC were obtained. Derivation and equations for obtaining radius of curvature are detailed in Yamashita (1996a). The circle of best fit is such that the height of triangle ABC (*h*) is less than or equal to half its base (*h* < *R*). As the height increases relative to the base, angle A becomes more acute. Though triangle AXY still describes the same circle as triangle ABC, points X

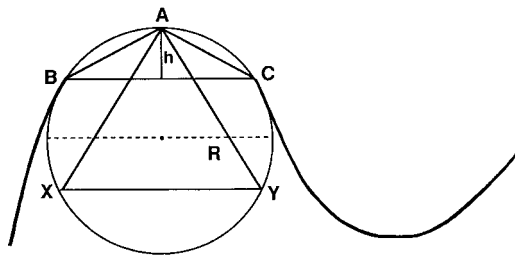


Fig. 3. Radius of curvature applied to schematic cusp. See text for explanation.

and Y are not on the cusp. Measurements of r obtained in the manner described above had high percentage errors but interspecific differences separated taxa.

Radius of curvature of basins were also determined. Point A was the lowest point of the basin, and the other two points were taken from the crests bounding the basin. Only radii of the trigon, trigonid, and talonid were measured. Points B and C were taken on the mesial and distal crests on the same Y-axis as point A.

Occlusal pairs. Ratios of radii of curvature (see above) and cusp and basin depths of occluding cusps and basins were determined. Basin depths were calculated with the Reflex scope and were measured as the height from the lowest point of the basin to a line joining the mesial and distal margins of the basin. These points were the midpoints of the crests delimiting the mesial and distal borders of the basin. In cases in which the distal crest is absent (trigon in most lemurs), the straight line distance demarcating the distal edge was used. In *Indri*, the central basin of the lower molar was measured in place of the talonid.

Occlusion ratios were calculated from logged raw data because ratios were calculated within a taxon and not between taxa. In both families, protocone/talonid and trigon/hypocone ratios were calculated. In addition, hypocone/trigonid ratios were calculated in indriids only; lemurs lack a hypocone.

Statistics

Several analyses had to be conducted prior to comparing tooth features with food properties. These included choosing an appropri-

ate size surrogate and clarification of variation in tooth features, such as scaling of individual tooth features and effects of taxonomic affiliation on variation. These analyses are presented in full in Yamashita (in press) and are summarized below.

Skull length and second lower molar area were both considered as potential size surrogates for bivariate regressions because actual body masses were unavailable for museum specimens. After consideration of both surrogates, lower molar area was chosen because it was a better predictor (higher correlation coefficients) of size when both were tested against actual body masses derived from a smaller sample of captive lemurs and field animals [skull length: $r = .601$; lower molar area: $r = .881$] (Glander et al., 1992; Terranova and Coffman, 1997).

Tooth features of lemurs and indriids were analyzed separately because analysis of covariance (ANCOVA) revealed differences between families in elevation of regression lines, although slopes were homogeneous (Yamashita, in press). Most tooth features scaled isometrically within families. Regressions were performed with individual tooth features contrasted with second lower molar area to check slope values. Since slopes were isometric, residuals were used as a means of size correction. Species means of every lemur species measured were used to obtain residual values against lower molar area for each tooth feature within each family. Comparisons with reduced major axis (RMA) were conducted initially, and, except in a few cases, both regression techniques yielded similar results. Subsequent analyses were conducted using least squares.

The taxonomic units of analysis in this study included well-established subspecies of lemur taxa. As a result, nonindependence of traits among closely related taxa was a concern. Closely related taxa share a recent common evolutionary history, and, therefore, the trait of interest may not have arisen independently in all the taxa examined (Harvey and Pagel, 1991). Although taxa within the Lemnidae and Indridae do not represent a single radiation (there are subspecies nested within species in each

family), nested ANOVAs conducted within families demonstrated that subspecies showed as much variance in some tooth features as species did. Interestingly, lemurs showed more variation occurring at the subspecific level than indriids (Yamashita, in press).

Finally, tooth features were analyzed with ANOVA to determine if they did indeed differ within families. Most of the comparisons were significant for lemurs, and less so for indriids.

Measurements of tooth features and tests of physical food properties form two distinct data sets. They were first compared with bivariate regression analysis in which logged mean hardness and shear strength values were contrasted with logged mean tooth features. The residuals of the five lemur taxa with dietary data were then regressed against physical food properties.

The mean values of the most stressful foods eaten (hardest, strongest) were analyzed separately from the most frequently eaten foods, as discussed in Hypotheses 4 and 5 above. The most stressful foods were limited to the single hardest and strongest foods eaten by each of the five species. The values of the most frequently eaten foods were determined by weighted averages: Average values for individual food items were multiplied by percentages of the total recorded time spent feeding on them within a season. The number of plant taxa tested for hardness and shear strength (second number) were *L. catta*, 10, 31; *P.v. verreauxi*, 7, 42; *P.d. edwardsi*, 18, 36; *L.f. rufus*, 19, 8; and *L. rubriventer*, 18, 7 (further detailed in Yamashita, 1996b). Because tooth features were measured per individual and physical food properties were pooled for species, values were averaged for the two data sets prior to regression analysis. This involved significant loss of data; therefore, a second analysis was employed.

Canonical correlation analysis (CCA) is a multivariate technique that compares multiple dependent variables (y) against multiple independent (x) variables. The objective of the CCA is to determine if the x and y sets of variables are related. The canonical correlation (R_c) is the most highly correlated linear combination of x and y variables.

Significant correlations indicate a relationship between the x and y variable sets (see Cooley and Lohnes, 1962; Vogt and Jameson, 1970; Levine, 1977; Neff and Marcus, 1980; Wilkinson, 1992, for more detailed discussions). Individuals of the five lemur taxa studied in the field were used in the CCA matrix. Residuals of tooth features were obtained from bivariate regressions against lower molar area conducted within each family as above. Residuals of the field taxa were then incorporated into a single CCA matrix (x variables) with the most frequently eaten and most stressful foods (y variables).

RESULTS

CCA and bivariate regression results mostly agree for specific tooth features (Tables 2, 3). The CCA results will be presented first, and the bivariate regressions will be discussed in terms of the CCA results. The first pair of canonical variates, r_c , are highly correlated (.8440) as is the second (.7286) (Table 2). The χ^2 results and F-value (5.7566, $P = 0.0000$) are also significant for the first four vectors of the CCA, demonstrating that there are significant correlations between tooth features and hardness and shear strength of foods. Clearly, the food properties tested and the teeth features measured are correlated.

The first canonical vector shows that as upper molar area (.9019) and upper molar basin area (.3071) increase but talonid area (−.4077) and cusp heights decrease, hardness values (both hardest and most frequent) decrease (−.8153, −.5025) and shear strength (both strongest and most frequent) increases (.9094, .2604). Hardness and shear strength have opposite signs on this first vector, and the extreme foods (hardest, strongest) have the highest loadings.

In the second canonical vector, upper molar basin area (.4296), talonid radius (.2352), and cusp heights increase as the hardest foods increase (.4741), and other areas and crest lengths decrease with the most frequently eaten hard foods (−.2045) and sheared foods (−.1725, −.5828).

Basin and tooth areas and M_2 cusp heights decrease on the third vector and crest lengths increase as the values of the hardest foods

TABLE 2. Results of canonical correlation analyses¹

	Matrix of correlations				
	X ₁	X ₂	X ₃	X ₄	
Upper molar basin area	0.3071	0.4296	-0.2954	-0.1145	
Upper molar area	0.9019	0.1605	-0.1008	0.1756	
Talonid basin area	-0.4077	-0.2432	-0.7438	0.1457	
Upper molar crest length	0.1866	-0.5312	0.1958	0.3574	
Lower molar crest length	-0.2577	-0.1225	0.3189	-0.0023	
Talonid radius	0.3127	0.2352	-0.1251	-0.0070	
Paracone height	0.0328	0.3677	0.0178	0.8036	
Metacone height	-0.2363	0.3222	0.1274	0.7526	
Protocone height	-0.3941	0.2170	-0.3862	0.2297	
Protoconid height	-0.2243	0.4343	-0.2749	0.3875	
Hypoconid height	-0.3438	0.4552	-0.2065	0.4212	
Metaconid height	0.0991	0.1657	-0.2304	0.3831	
	<u>Y₁</u>	<u>Y₂</u>	<u>Y₃</u>	<u>Y₄</u>	
Hardest	-0.8153	0.4741	0.3324	-0.0069	
Freqhard	-0.5025	-0.2045	-0.7404	0.3969	
Strongest	0.9094	-0.1725	-0.3769	0.0336	
Freqstrong	0.2604	-0.5828	-0.5236	0.5643	
Root	r _c	r _c ²	χ ²	d.f.	P value
1	.8440	.71	208.5040	48	.0000
2	.7286	.53	109.4329	33	.0000
3	.5662	.32	49.2673	20	.0003
4	.4560	.21	18.5352	9	.0294
Wilks' lambda = .0726					
F = 5.7566					
d.f. = (48, 283) P = .0000					

¹ Tooth features are defined in Figures 1, 2 and the Appendix.

increase (.3324) and the most frequently eaten hard foods (-.7404) and sheared foods decrease (-.3769, -.5236).

Cusp heights and upper molar crest length increase on the fourth vector with the most frequently eaten hard foods (.3969) and most frequently eaten sheared foods (.5643).

CCA and bivariate regressions yield similar results (Tables 2, 3). Basin areas have the same relationships with hardness and shear strength; upper molar basins are positively related to shear strength and lower molar basins to food hardness. Compared to the first CCA vector, crest lengths are positively related with the hardest foods in the bivariate regressions. Crest lengths differ more in the second and third CCA vectors, but whereas in the CCA the results are equivocal with respect to hardness, in the bivariate regression crest lengths are negatively related to frequently eaten hard foods and especially to frequently eaten sheared foods. Cusp heights are generally positively associated with hardness and negatively associated with strong foods in both the bivariate regressions and the CCA, at least in the first two vectors.

DISCUSSION

Because only five lemur taxa had both the mechanical properties of their foods tested and their tooth features measured, the resulting bivariate regressions and correlations must be interpreted cautiously. Because the CCA and bivariate results were similar, the discussion will be confined to the bivariate results. Relationships between molar features and food properties (Tables 2, 3) are discussed in terms of the hypotheses below. Mechanical dietary characterizations of lemur taxa are presented in Yamashita (1996b).

Hypotheses

The null hypothesis is rejected on the basis of the significance of the canonical correlation analysis and on the strength of the correlation coefficients between individual tooth features and different sets of mechanical food properties. Hardness and shear strength do have a relationship to tooth form. This relationship, however, is not as straightforward as originally hypothesized. Each hypothesis is discussed in de-

TABLE 3. Bivariate correlations of tooth features and food properties¹

Tooth feature	Hardest	Freqhard	Strongest	Freqshear
Upper molar basin area	-0.993	-0.054	0.934	0.738
Upper molar area	-0.785	-0.589	0.901	0.209
Talonid basin area	0.449	0.580	-0.345	-0.308
Upper molar crest length	0.183	-0.679	0.051	-0.756
Lower molar crest length	0.741	-0.459	-0.759	-0.787
Total crest length	0.550	-0.667	-0.392	-0.949
Paracone height	-0.176	-0.042	-0.003	-0.161
Metacone height	0.294	0.035	-0.494	-0.410
Protocone height	0.274	0.811	-0.441	0.138
Protoconid height	0.020	0.526	-0.213	0.068
Hypoconid height	0.183	0.415	-0.380	-0.126
Metaconid height	-0.364	0.651	0.331	0.427
Paracone radius	0.688	0.509	-0.805	-0.024
Metacone radius	0.846	0.431	-0.700	-0.369
Protocone radius	0.459	0.414	-0.436	0.198
Protoconid radius	-0.070	0.651	0.139	0.655
Hypoconid radius	-0.551	0.096	0.275	0.710
Metaconid radius	-0.401	-0.297	0.137	0.091
Trigon depth	0.588	0.883	-0.650	0.077
Trigon radius	0.006	-0.960	0.062	-0.661
Talonid depth	0.261	-0.231	0.045	-0.567
Talonid radius	-0.514	-0.904	0.490	-0.059
Protocone/talonid radii	0.356	-0.095	-0.461	0.033
Hypoconid/trigon radii	-0.239	0.543	0.007	0.780

¹ Tooth features are defined in Figures 1, 2 and the Appendix.

tail below, first in terms of how the empirical relationship matches expectations. Then, details of the interspecific pattern are examined, especially where they depart from expected relationships.

Hypothesis 1: Crest length is positively correlated with food shear strength.

Crest length was thought to be directly related to leaf strength because of mechanical considerations involved in fracturing leaves. Although leaves share a common geometry, they vary in their mechanical properties as a result of differences in water

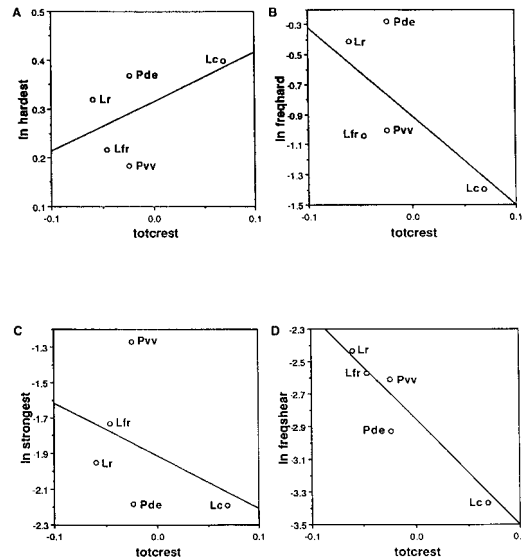


Fig. 4. Bivariate regressions between summed total crest length and food properties. Correlation coefficients are as follows: (A) $r = 0.550$, (B) $r = -0.667$, (C) $r = -0.392$, (D) $r = 0.949$. See Figures 1–3 for further explanation.

content, venation, and thickness (Lucas et al., 1991), all of which can affect leaf toughness, or the amount of work needed to fracture them. Longer crests would be able to drive crack propagation in tougher leaves, much as carnassial teeth in carnivores slice tough meat particles.

However, from the lack of positive correlations between shear strength and crest length in the CCA and bivariate regressions, crest length does not appear to be dictated by the strength of the leaves consumed in the diet (Fig. 4). The taxa with the longest crests (the two indriids and *L. catta*) have a folivorous diet in common, but most of the leaves they eat are immature and therefore weak and brittle. This contributed to the weak correlation of crest length to shear strength in the CCA (Table 2) and the strong negative correlation in the bivariate regressions (Table 3). Some attribute of leaves must be related to the best method of processing them. Sheine and Kay (1982) hypothesized that crest length was related to dietary fiber content. Although this relationship was not explicitly addressed in the present study, fiber content probably contributes to toughness in foods such as

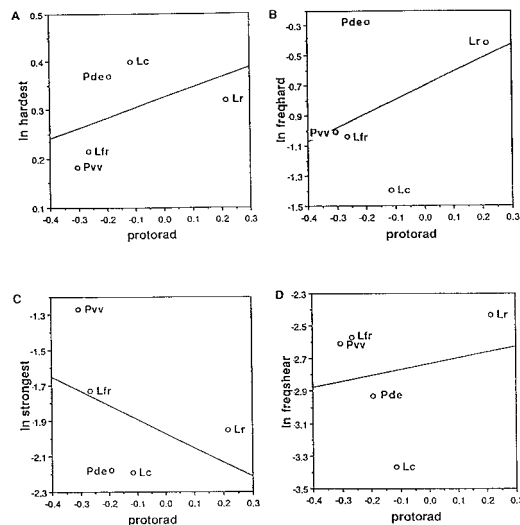


Fig. 5. Bivariate regressions between cuspal radius and food properties represented by protocone radius. Correlation coefficients are (A) hardest foods = 0.459, (B) most frequently eaten hard foods = 0.414, (C) strongest foods = -0.436, (D) most frequently sheared foods = 0.198. freqhard, frequently eaten hard foods; freqshear, frequently sheared foods; Lc, *Lemur catta*; Lfr, *Lemur fulvus rufus*; Lr, *Lemur rubriventer*; Pde, *Propithecus diadema edwardsi*; Pvv, *Propithecus v. verreauxi*. See Figures 1, 2 for further explanation.

mature leaves. Presumably, diets strong in shear are tough and high in fiber. The lack of correlation between shear strength and crest length would also extend to fiber content.

Looking within families, *L.f. rufus* and *L. rubriventer* have shorter crests than *L. catta*, but both occasionally eat stronger leaves. Because *L.f. rufus* ate strong leaves in the dry season and, according to Sussman (1974), other populations of *L.f. rufus* are more folivorous than those studied at Ranomafana (in Yamashita, 1996b), it appears that the secondary component of its diet (strong leaves) is not a significant determinant of crest length. *L. catta* has the longest crests among the lemurids, and its cusps are more acute than those of *L. rubriventer*; another lemurid that eats hard foods (Fig. 5). The combination of long crests and acute cusps has been associated with a folivorous diet (Seligsohn, 1977), and *L. catta* is indeed the most folivorous of the lemurids studied.

Indriids have longer crests than lemurids at the same tooth size (Yamashita, 1996a). Comparing the indriids, *P.d. edwardsi* has short upper molar crests but is otherwise

undifferentiated from other indriids (Yamashita, 1996a). Although *P.d. edwardsi* was less folivorous than *P.v. verreauxi*, it still included leaves in its diet (30% in both seasons for *Pde*, 79–66% between wet and dry seasons for *Pvv*). Although *P.v. verreauxi* feeds on strong leaves, its crests are not longer than those of other indriids. Neither the relative strength nor the higher amounts of leaf material in its diet are reflected in its crest lengths (discussed below).

Modes of failure for solids depend on their physical makeup and their geometry. Because leaves are flat sheets of material, the most efficient method of processing them is by elaborating crests or lophs, as ruminants have done. Increased crest length appears to solve the geometric problem posed by leaves rather than that of their material composition. This supports earlier observations linking crest length with degrees of folivory (Kay, 1975). Stated another way, a certain amount of leaf material has to be consumed before a morphological response is triggered. As noted earlier by Seligsohn (1977), leaf eating, regardless of material composition, forms its own distinctive physical category.

To test this supposition, crest lengths of the five field taxa were regressed against percentages of feeding time for both seasons individually and averaged across seasons. Whereas crest lengths were negatively correlated with shear strength (Tables 2, 3), crest lengths regressed against percentages of folivory averaged across seasons were positively associated for upper molar crest ($r = .687$) and total crest lengths ($r = .255$) and (unexpectedly) negatively related to lower molar crest length ($r = -.436$). Correlation coefficients for wet and dry seasons followed the same patterns.

The question remains whether overall degree of folivory is important or whether leaf consumption at key times of the year is the determining factor. Based on the relative degree of folivory of the taxa with long crests versus those without, the minimum percent feeding time needed for crest length to be increased lies between the feeding percentages of *Lemur catta* and *Lemur rubriventer*. *L. catta*, the most folivorous of the lemurids, spent 44% feeding time on leaf material in

the wet season and 15% in the dry. *L. rubriventer* spent the most feeding time on leaves among taxa without long crests, 10% in the wet season and 3% in the dry. It is not clear whether the minimum feeding time of each is the relevant contrast (15% vs. 3% during the dry season when the strongest foods were eaten) or whether the percentages when leaves were eaten most frequently (44% vs. 10%) is relevant.

Hypothesis 2: The radius of curvature (r) of cusps is positively correlated with the hardness of foods. As noted earlier, hard diets are expected to be correlated with blunt cusps to minimize wearing of cusp tips and to maximize crack propagation with a greater surface area applied to hard food objects. This hypothesis is supported in the upper second molar only (Table 3). Lemurs which eat the hardest foods have the highest radii of curvature of the three upper molar cusps. In contrast, shear strength is negatively associated with cusp acuity in the upper molar cusps (Fig. 5C; Table 3). Those lemurs which eat foods with high shear strength have acute cusps (*P.v. verreauxi* and *L.f. rufus*), though not all lemurs with acute cusps eat strong foods (*L. catta*). The lower molar cusps show the opposite pattern: Blunt cusps are associated with shear strength and acute cusps with the hardest foods.

How can these patterns be interpreted? One of the complications in examining tooth morphology is that each feature is part of an interdigitating system. Acute cusps are also related to loose cusp-to-basin occlusal fit. All three taxa with acute cusps have loose occlusion within their families achieved by the acuity of their cusps (Figs. 9, 10). In the case of *L. catta*, the hypoconid/trigon ratio is the lowest (loose fit) among the lemurids and is related to its frequent diet of weak leaf material (Fig. 10) (see discussion of Hypothesis 3).

Although *P.d. edwardsi* has blunter cusps than *P.v. verreauxi*, *P.d. edwardsi*'s cusps are more acute than its conspecifics. This suggests that, whereas the hard food-blunt cusp relationship may be accurate for lemurids, cusp acuity in indriids is more complicated and, perhaps, related to the morphology of their crests. *P.d. edwardsi* eats both

hard and weak foods frequently, which was initially surprising given the acuity of its cusps. In *P.d. edwardsi*, cusp acuity is negatively correlated with crest length for most of the cusps (Yamashita, 1996a). For indriids as a whole, however, cusp radii and crest lengths are positively correlated (Yamashita, 1996a). Acute cusps in *P.d. edwardsi* may result as a consequence of decreasing crest length because it has short crests relative to other indriids.

Alternatively, although a diet of seeds and leaves such as *P.d. edwardsi* consumes initially appears to require distinctly different morphologies, Lucas and Teaford (1994) describe how bilophodont colobine molars are suited to a diet of young leaves (soft, brittle foods) and tough seeds. Molar crests of colobines combine wedges formed by the cross-lophs with buccal and lingual crests or blades (Lucas and Teaford, 1994). It was hypothesized that the wedges split apart tough seeds and the sharp crests broke down leaf material. Crests that act as wedges present a larger surface for fracturing hard food items than acute cusps which have a small surface area that transmits high localized forces. Seed-eating has also been studied in cercopithecines in which the central basin of the lower molars were hypothesized to hold the seed in place while the occluding molar shattered it (Happel, 1988). If the bilophs are viewed in this way, flat leaves and hard seeds are not a mechanically contradictory diet. Like cercopithecids, indriids possess bilophodont molars, culminating in those of *Indri indri* (Schwartz and Tattersall, 1985). Other recent field studies on indriids have confirmed a preference for seed eating in sympatric *P.d. diadema* and *I. indri* (Powzyk, 1996). The presence of bilophodonty in indriids may be related to just such a functional complex as described for colobines.¹

¹The relationship between seed eating and body size also needs to be considered. *P.d. edwardsi* may be able to eat a hard diet simply by virtue of its relatively greater body size and the absolutely greater muscular forces it can generate. *P.d. edwardsi* is approximately twice the size of *P.v. verreauxi* (5,743 g compared to 2,720 g; weights from Glander et al., 1992; Yamashita, 1996a). However, the hard-object feeder in Kinzey and Norconk's (1990) study, (*Chiropotes satanas*, 2,980 g), was smaller than the sympatric *Ateles paniscus* (9,000 g) which ate a softer diet (weights from Fleagle, 1988). The size range in Happel's (1988) study on five cercopithecine taxa ranged from *Cercopithecus campbelli* to *Papio papio*, yet preferences for hard foods did not differ among the species.

The co-occurrence of seed-eating and bilophodonty in *P.d. edwardsi* matches the pattern found in cercopithecids, and *L. rubriventer*'s blunt cusps support predictions related to eating a hard diet. Although both eat hard foods, their different morphologies suggest that there is more than one morphological solution to the same biomechanical problem.

In addition to cusp acuity, cusp height is also positively correlated with hard foods and negatively with strong foods when all field taxa are considered (Table 3). Among lemurids, however, cusp heights are negatively associated with hard foods and positively with strong foods (Fig. 6). Hypsodonty (high crowns) is found in mammalian taxa with abrasive herbivorous diets and has been related to the wear these diets produce (Janis and Fortelius, 1988). The lemurid-only pattern fits the hypsodont profile to some extent. *Lemur fulvus rufus* has higher cusps than the other two and eats a slightly stronger diet.

The two indriids are responsible for the general pattern in which high cusps related to hard diets and low cusps to strong diets (Fig. 6). *P.d. edwardsi* has high cusps, but this is probably not related to food abrasiveness as *P.v. verreauxi* has a more folivorous, stronger diet and yet has shorter cusps. Lucas and Teaford (1994) cited the greater occlusal relief of colobines as a means of achieving longer crest lengths for comminuting leaves. *P.d. edwardsi*, however, has a less folivorous diet than *P.v. verreauxi*, and its crest lengths are shorter than other indriids. Its high cusps could be related to the combined demands of a hard and folivorous diet. In a taxon that maintains crest length (as do all indriids) yet eats a hard diet, perhaps a high crown affords some protection against wear. Janis and Fortelius (1988) discussed how thick enamel was not an option for taxa with sharp crests because thick enamel blunts tooth features. Increasing cusp heights may be a means of increasing the wear resistance of the occlusal surface. In contrast, *L. rubriventer* does not have the problem of maintaining its crests and handles its hard diet with blunt cusps. Molnar and Gantt (1977) related blunt cusps with thicker enamel. Lower molar buccal

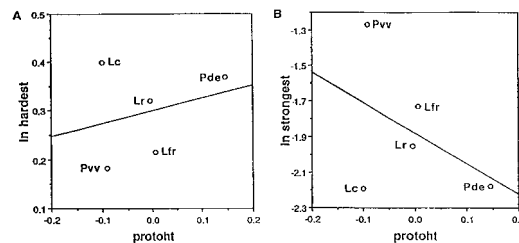


Fig. 6. Bivariate regressions between cusp height and food properties represented by protocone height. Correlation coefficients are (A) hardest foods = 0.274, (B) strongest foods = -0.441. See Figures 1–3 for further explanation.

cusps of *Macaca* had thicker enamel, and by implication blunter cusps, than the higher, acute cusps on the lingual side. If blunt cusps have thicker enamel, then low cusps (or low relief) would be a consequence of this thickening. The two taxa with the most frequently eaten hard diets apparently pursue different means of dealing with the problem of attendant tooth wear.

Hypothesis 3: Basin area increases relative to cusp radius as food hardness increases, and cusp-to-basin ratios decrease with increasing food hardness. Food hardness was predicted to be correlated with increasing basin area to allow for greater excursion of the cusp in its occluding basin to find and exploit the weakest points of hard food particles. This expected relationship between basin area and hardness was found to be only partially correct. Upper and lower molar basin areas show opposite correlations to the two physical properties in both the CCA and bivariate analyses (Tables 2, 3). Hardest foods are highly negatively correlated with upper molar basin area (Fig. 7) and positively related to talonid area (Fig. 8). Strongest foods show the opposite pattern. They are positively related to upper molar basin area (Fig. 7) and negatively to talonid area (Fig. 8).

Correlations between occlusal pairs are not particularly strong (Table 3). Ratios of the protocone/talonid radii are positively associated with the hardest foods but negatively with the strongest (Fig. 9). Hypoconid/trigon ratios show the opposite pattern; they are most highly positively correlated with the most frequently eaten hard foods and

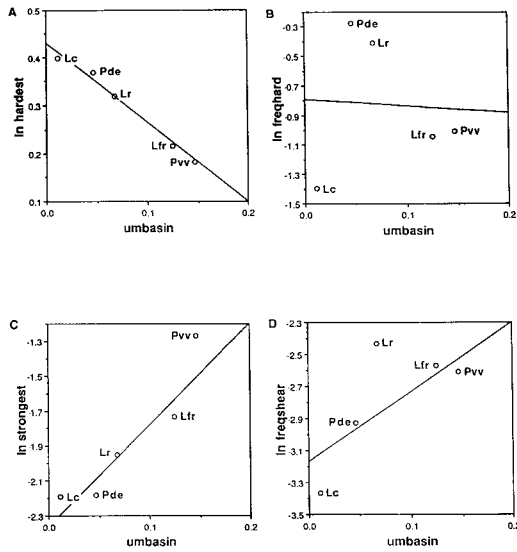


Fig. 7. Bivariate regressions between upper molar basin areas (trigon + talonid) and food properties. Correlation coefficients are as follows: (A) $r = -0.993$, (B) $r = -0.054$, (C) $r = 0.934$, (D) $r = 0.738$. See Figures 1–3 for further explanation.

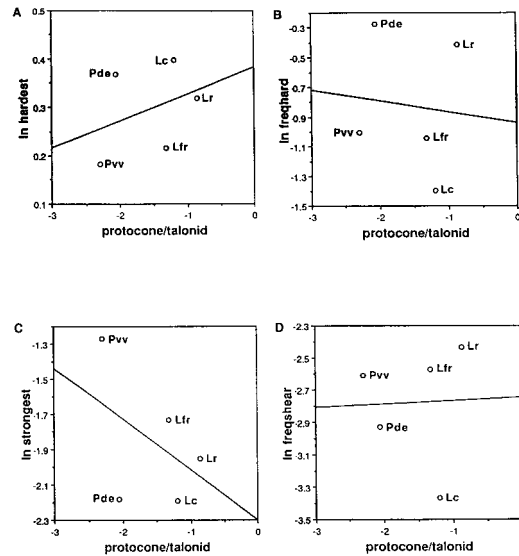


Fig. 9. Bivariate regressions between protocone/talonid radii ratio and food properties. Correlation coefficients are as follows: (A) $r = 0.356$, (B) $r = -0.095$, (C) $r = -0.461$, (D) $r = 0.033$. See Figures 1–3 for further explanation.

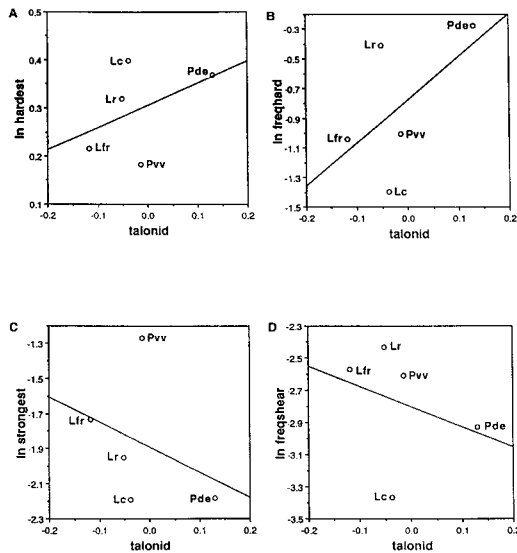


Fig. 8. Bivariate regressions between talonid area and food properties. Correlation coefficients are as follows: (A) $r = 0.449$, (B) $r = 0.580$, (C) $r = -0.345$, (D) $r = -0.308$. See Figures 1–3 for further explanation.

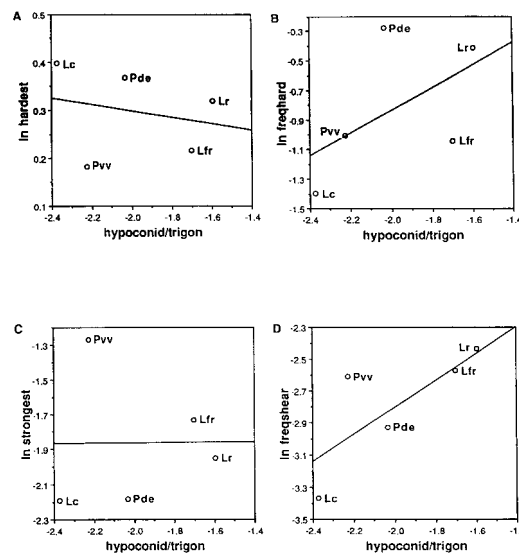


Fig. 10. Bivariate regressions between hypoconid/trigon radii ratio and food properties. Correlation coefficients are as follows: (A) $r = -0.239$, (B) $r = 0.543$, (C) $r = 0.007$, (D) $r = 0.780$. See Figures 1–3 for further explanation.

sheared foods and negatively associated with the hardest foods (Fig. 10).

Higher occlusion ratios indicate greater tightness of fit of the occluding elements. Hardness, either the hardest food or most

frequently eaten hard food, is positively correlated with both occlusal pairs, so that as occlusal fit becomes tighter, food hardness increases. The two occlusal pairs express opposite correlations with shear

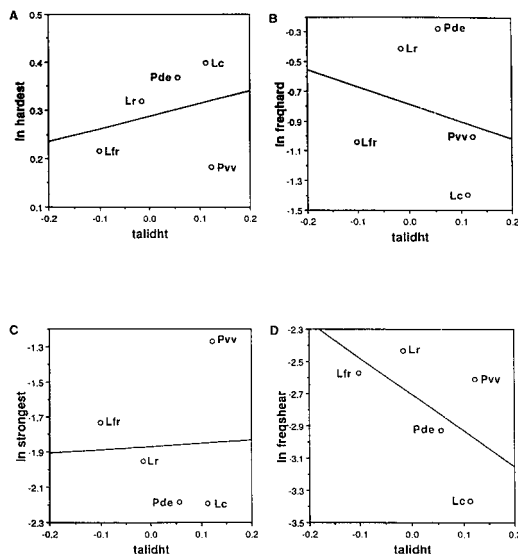


Fig. 11. Bivariate regressions between talonid depth and food properties. Correlation coefficients are as follows: (A) $r = 0.261$, (B) $r = -0.231$, (C) $r = 0.045$, (D) $r = -0.567$. See Figures 1–3 for further explanation.

strength. *L. rubriventer* and *P.d. edwardsi* have the tightest occlusal fit relative to the other field taxa within their respective families (Figs. 9, 10). The blunter cusps of these two taxa are related to the hard foods they eat frequently (Fig. 5). As discussed above, hard foods were expected to be related to a loose occlusal fit and also with blunt cusps. These expectations do not have to be contradictory if basin size increases relative to its occluding cusp. However, cusp acuity usually determines the occlusion ratio, and hard foods are correlated with blunt cusps. The positive relation between hard foods and tight occlusal fit appears related to food entrapment. The advantage of trapping foods, especially brittle foods, in relatively small basins is that they can be held in place for blunt cusps to shatter them.

L. catta, *P.d. edwardsi*, and *P.v. verreauxi* have deep lower molar basins (Fig. 11). Because these three taxa ate weak, brittle leaves frequently (they were the most folivorous of the five taxa studied), the presence of a deep talonid could be related to this diet. A deep basin can act as a food retainer. The talonid, as the major basin of the lower molar, would confine foods for continued breakdown. Weak, brittle leaves require little

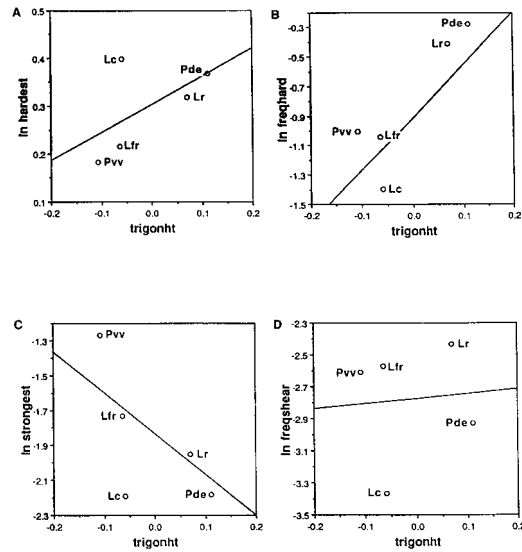


Fig. 12. Bivariate regressions between trigon depth and food properties. Correlation coefficients are as follows: (A) $r = 0.588$, (B) $r = 0.883$, (C) $r = -0.650$, (D) $r = 0.077$. See Figures 1–3 for further explanation.

pressure to break them down, and efficiency would best be served by “batch processing” in the basins (Lucas and Luke, 1984), wherein multiple food particles would be trapped in the basins and processed at a single time.

Correlations with hardness and feeding frequency of weak foods converge in basin depths. Trigon basin depth is negatively correlated with the strongest foods and positively correlated with the hardest foods eaten (Fig. 12). Hard foods require deep basins for the same reasons that weak foods do, for food retention. Although the opposite was initially hypothesized, trapping hard foods would maximize particle breakage with every chew. If the food were brittle, shatter could be most efficiently effected by a blunt cusp fitting snugly into the basin.

Shallow, broad basins were initially predicted for hard foods in order to allow greater excursions of cusps in basins. This morphology was instead found for strong foods. Breaking down foods that are flat and strong would require a flat surface and consecutive shearing by crests in the manner of a “milling machine.” Shallow basins would not retain foods. Food retention would be disadvantageous because the desired result is to

expose the food surface to as many crests as possible. Because strong leaves are two-dimensional, breakdown with a mortar-and-pestle would not be an efficient means of triturating them.

In sum, hardest foods are correlated with deep, acute basins and large talonid areas but small trigons. Taxa which eat the strongest foods and soft foods have unconfined talonids (shallow, blunt) but small areas and shallow, large, acute trigons. Frequently eaten sheared foods (generally weak foods) are related to deep basins.

Most frequently eaten versus critical foods

Hypothesis 4: Crest length is more highly correlated with the shear strength of the strongest food eaten than with the most frequently eaten food. Correlations between shear strength and crest lengths are mostly negative. This is due almost entirely to the position of *L. catta* in the bivariate regressions (Fig. 4) which has long lower molar crests but a diet weak in shear. Correlations between crest lengths and the most frequently eaten foods are higher than correlations with the strongest foods. In fact, the correlation between frequently sheared foods and total crest length has the highest, *negative* value ($r = -.949$). The canonical correlations show opposite correlations between crests and food values (Table 2), wherein upper molar crest length is generally positively correlated with shear strength and lower molar crests are positively correlated with hardness, which agrees with the bivariate results (Table 3). Hardest foods are positively correlated with crest lengths in bivariate regressions (Table 3; Fig. 4). The hypothesis as stated is not supported.

Hypothesis 5: The radius of curvature of cusp tips is more highly correlated with the hardest food eaten than with the hardness value of the most frequently eaten food. Cusp radii and the hardest foods eaten have higher correlation coefficients than cusp radii and the most frequently eaten hard foods (Table 3; Fig. 5). However, the most frequently eaten foods are more consistently positively correlated with cusp radii (Table 3). Strongest foods

eaten are negatively correlated with M^2 cusp radii, so that the higher the shear value of the food, the more acute the cusp tip (Table 3; Fig. 5C). Frequently sheared foods are generally not as highly correlated with cusp acuity (Fig. 5D).

The hypothesis as stated is supported with modifications. The hardest foods are more highly positively correlated with the radius of curvature of cusp tips than the most frequently eaten hard foods for the M^2 . Lower molar cusps are more varied in correlations with food properties. They are negatively correlated with the hardest foods (more acute) and positively correlated with shear strength (blunter). These correlations are not as high as those with the M^2 cusps.

In the contrasts above, the extreme foods and most frequently eaten foods were equally highly correlated with tooth features in the bivariate regressions (Table 3). According to the CCA (Table 2), however, the most stressful foods generally had higher correlations with tooth features than the most frequently eaten foods in the first two vectors. Considering the degree of overlap in ranges of food property values, the lack of a strong correlation for either the most stressful or most frequent foods is not surprising.

Hard foods apparently incur differences in morphology depending on how frequently they are consumed, perhaps imposing a greater variety of effects on tooth features than shear strength taken as a single category. Shear strength values are not separated, which may indicate that these foods are more constrained to a single morphology. The dichotomy of food values in the CCA is between the hardest foods and all other properties.

The question of whether the most frequently eaten diet or the most stressful diet is more highly correlated with tooth form is connected to compromises in morphology. The five taxa studied in the field did not have mechanically homogeneous diets (Yamashita, 1996b), especially in comparisons of the most frequently eaten foods and the extremes of dietary ranges. The bulk of the diets among the five taxa overlapped considerably with one another, even among taxa that inhabited different sites. Because of this variability in diets, lemur teeth almost

have to compromise to be at least "adequate" (sensu Gans, 1993) for the extremes of dietary ranges. Judging by the patterns of correlations of tooth features with food properties, tooth features of some taxa are more highly correlated with their "modal" diet and others to the extremes of their diet.

It was hypothesized that during periods of food scarcity animals would eat at the extremes of their dietary ranges to separate themselves from competitors. The tooth features related to these foods would presumably be strongly selected during periods of stress (drought, seasonal differences in food availability), and the most frequently eaten foods (if they were not the hardest or strongest) would not be as great a determinant of tooth morphology. The hardest and strongest foods in the diets of the five taxa did separate them (Yamashita, 1996b). Although the most stressful and most frequently eaten foods are correlated with tooth features, the most stressful foods have overall higher correlations.

Molars are all-purpose tools as reflected by individual tooth features. Even among taxa as uniform in molar form as indriids, secondary dietary components are correlated with tooth features, much as Kinzey (1978) and Rosenberger and Kinzey (1976) demonstrated for some platyrrhine species. The common condition is to be heterogeneous to enable trituration of mechanically diverse diets.

Functional complexes

Individual tooth features have specific relationships to food properties, and some tooth features tend to co-occur in relation to an identifiable functional role; i.e., they form functional complexes. Basin configurations (depth and radius) are consistently negatively correlated across taxa for most of the basins examined (Yamashita, 1996a). In addition, ratios of cusp acuity to basin acuity are indicators of loose versus tight occlusal fit. Loose occlusal fit is related to strong diets, and tight fit is related to hard diets. In lemurids, short cusps that are also blunt in the M² are also correlated with a diet of hard food items. When these features are assembled for any one diet, they describe a certain type of molar architecture quite well.

Shallow, flat basins, large upper basins, and small talonids appear in taxa that eat strong foods to varying degrees. Soft, brittle foods are correlated with the same features as strong foods for the most part. As leaf shape is most likely the significant physical property of leaves, strong and weak leaves should be correlated with the same morphologies. Hard foods are correlated with short cusps in lemurids, tight occlusal fit, small trigon and large talonid areas, and deep, acute basins.

Correlations among congeners

The most closely related taxa studied, *L.f. rufus* and *L. rubriventer*, differ in physical food properties, choice of food items, and in certain tooth features. Both taxa are primarily frugivorous, but *L.f. rufus* concentrates on soft fruits and *L. rubriventer* on hard fruits. When leaf material is included in the dry season, *L.f. rufus* eats stronger leaves than *L. rubriventer*. These differences in diet are evident in their molar morphologies. *Lemur rubriventer's* harder diet is reflected in its blunter, shorter cusps and deep trigon basin. The infrequent inclusion of strong foods in the diets of both taxa can be seen from their large trigon areas and shorter-than-expected crest lengths. Higher cusps in *L.f. rufus* are indicative of its slightly stronger diet.

P.d. edwardsi and *P.v. verreauxi* have the characteristic indriid molar dominated by crests. However, their overall diets are quite dissimilar, as reflected in their cusp and basin morphologies. *P.d. edwardsi* is a hard object feeder and eats soft/brittle foods (weak leaves). *P.v. verreauxi* is elasticophagus (strong leaves) and supplements its diet with soft/brittle foods (soft fruits, weak leaves). *P.d. edwardsi* has larger lower molar areas, higher cusps, deeper trigon and trigonid basins, and tighter occlusal fit of cusps and basins than *P.v. verreauxi*. *P.v. verreauxi* has larger upper molar basin and tooth areas, more acute cusps, a deeper talonid, and a looser occlusal fit than *P.d. edwardsi*.

The presence of long crests in all indriids may be explained as a product of some past adaptive event. The long crests may have been maintained in the group because they

continued to have the original function (stabilizing selection) or the existing morphology had been successfully co-opted for different functions. In support of the maintenance of the crests by stabilizing selection, all indriids that have been studied in the field are reportedly folivorous to some extent (Pollock, 1977; Richard, 1978; Ganzhorn, 1988, 1989; Meyers and Wright, 1993; Powzyk, 1996). The long crests may be a response to continued selection for comminuting flat leaves, if they indeed originally evolved for this purpose. *L. catta* is the most folivorous lemurid studied and it, too, has long crests. However, while *P.d. edwardsi* and *P.v. verreauxi* are folivorous (although to different degrees), their overall diets are quite different. As discussed above, crest length in *P.v. verreauxi* is correlated with its mostly folivorous diet, whereas crests in *P.d. edwardsi* appear to have been co-opted for seed-eating. The morphology appears to be robust to taking on new functional roles.

These differences in both dietary properties and dental diversity between close relatives argue for a detailed examination of closely related taxa to parcel out the effects of environmental variables on morphology. To emphasize this point, Ungar (1996) similarly found a stronger relationship between large incisors and frugivory among closely related anthropoids rather than between more distantly related taxa.

SUMMARY AND CONCLUSIONS

Food properties and tooth features are significantly correlated, with the strength of the correlation depending on the tooth feature. Earlier work on functional morphology had assumed that some physical component of foods was related to tooth form. This study explored specific hypotheses of relationships between tooth features and food properties and found that food properties bear a direct relationship to tooth form. However, the details of the interactions demonstrate a need for caution in generalizing these results because of the small sample size and exceptions to the overall pattern as discussed. For the specific hypotheses: 1) crest length is negatively correlated with strong foods instead of the expected positive correlation. Crest lengths are related to

quantities of leaf consumption which are related more to leaf geometry than material composition. 2) Radius of curvature of cusps is positively correlated with food hardness and negatively with shear strength. 3) Hard foods were expected to be correlated with loose fit of occluding cusps and basins. Instead, ratios of occluding cusp-to-basin radii demonstrate that tight occlusal fit is related to a hard diet and loose fit to strong foods.

The specific association of cusp radii to food hardness shows that the most stressful foods (hardest foods) are more highly correlated with cusp radii than the most frequently eaten foods. However, neither hardness nor shear strength demonstrates strong correlations with crest lengths no matter how frequently eaten or stressful. With regard to other features, the conclusion is equivocal; although the most stressful foods have higher correlations with tooth features, the most frequently eaten foods are also, less strongly, correlated. Generally speaking, overall molar morphologies of the five taxa studied are indicative of the most stressful foods eaten.

Thus, there is some basis for claiming that the most stressful foods maintain separation among taxa, especially because tooth features are more highly correlated with them. The majority of foods tested for hardness, however, are well within the limits of all five taxa. Therefore, despite differences in tooth morphology, their teeth are adequate for masticating most of the foods tested. This suggests that teeth can tolerate diets with a wide range of physical properties without accompanying changes in morphology. The complexities involved in teasing apart the functional relationships of molars and foods may be related to the multitude of ways in which foods can be characterized (only two were considered here) and to selection acting on nondental morphologies involved in food processing, such as the gastrointestinal tract.

Nevertheless, several functional complexes are identified that describe certain co-occurrences of tooth features related to specific diets. Hard foods are related to short cusps in lemurids, tight occlusal fit, small trigon and large talonid areas, and deep, acute basins. Large, shallow trigons and

shallow, unrestricted talonids are indicative of diets strong in shear. Relationships between cusp acuity and the two food properties depend on the cusp and its position in the upper or lower molar. Soft, brittle foods are correlated with the same features as strong foods for the most part. The correlates found here may be generalizable to other taxa if their molar morphologies can be contrasted to those of closely related forms. Further testing of other taxa will determine the wider applicability of the patterns noted.

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